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THE RESPONSE OF SUBALPINE FORESTS TO SPRUCE BEETLE OUTBREAK IN COLORADO[1]

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Abstract. Spruce beetle (*Dendroctonus rufipennis* Kirby) outbreaks are important disturbances affecting subalpine forests of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*) in the southern Rocky Mountains. However, little is known about the influences of these outbreaks on overall forest dynamics. We used age-structure analyses and dendrochronological techniques to investigate the effects of a major spruce beetle outbreak on stand composition, dominance, tree age and size structures, radial growth, and succession in subalpine forests in Colorado. This outbreak, which occurred in the 1940s, caused a shift in dominance from spruce to fir and a reduction in average and maximum tree diameters, heights, and ages. The outbreak did not favor new seedling establishment of the seral lodgepole pine. Thus, in seral stands spruce beetle outbreak accelerates succession towards the shade-tolerant tree species.

The predominant response to the outbreak was the release of previously suppressed small-diameter spruce (not attacked by the beetle) and subalpine fir (a non-host species). Following the 1940s outbreak, growth rates of released trees remained high for >40 yr. The relative increases in growth rates were similar for both species. Both spruce and fir will continue to codominate the affected stands. The predominance of accelerated growth following a spruce beetle outbreak, instead of new seedling establishment, is a major contrast to the pattern of stand development following fire. In some Colorado subalpine forests the effects of disturbance by spruce beetle outbreaks appear to be as great as those due to fire.

Key words: Abies lasiocarpa*; age structure; Colorado Rocky Mountains;* Dendroctonus rufipennis*; dendroecology; disturbance;* Picea engelmannii*; spruce beetle outbreak; spruce–fir forest; subalpine forests; succession.*

INTRODUCTION

Episodic outbreaks of insects lethal to particular tree species are common in many temperate forests (Morris 1963, Furniss and Carolin 1977, Schowalter 1985). Massive tree mortality from these outbreaks releases resources that potentially are available to survivors of the outbreak or to individuals that subsequently become established. Thus, in addition to the direct effects of the mortality, outbreaks are likely to affect tree growth rates and establishment patterns, which in turn may alter stand productivity, structure, and composition (Morris 1963, Amman 1977, Romme et al. 1986). Changes in stand development patterns often result from interactions among lethal insects, pathogenic fungi, and fires (Knight 1987).

Fire, blowdown, and insect attack in Rocky Mountain coniferous forests create mosaics of stands of varying structure and composition (Peet 1988). In the subalpine forests of Colorado (i.e., above ≈2750 m), characterized mainly by Engelmann spruce (*Picea engelmannii* (Parry) Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) (Nutt.), quaking aspen (*Populus tremuloides* Michx.) and lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), fire is believed to have been historically the most important form of natural disturbance (Clements 1910, Romme and Knight 1981, Peet 1988). Consequently, there have been numerous investigations of stand development patterns following wildfire in the subalpine zone (e.g., Whipple and Dix 1979, Peet 1981, Romme and Knight 1981, Romme 1982, Veblen 1986*a*). These studies document the gradual replacement of the seral pines and aspen by fir and spruce, although the patterns vary markedly according to habitat and seed availability.

Widespread disturbance by spruce beetle (*Dendroctonus rufipennis* Kirby) outbreaks is well documented for the southern Rockies (Schmid and Frye 1977, Schmid and Hinds 1984) where spruce beetle outbreaks may be as ecologically significant as fire (Baker and Veblen 1990). However, we know surprisingly little about the influence of these outbreaks on overall forest dynamics. To address this gap in our knowledge we designed a study of the effects of spruce beetle outbreaks on stand composition and dominance, age and size structure, tree growth, and succession. We examined stand responses, over a range of site conditions and pre-attack stand structures, to the severe spruce beetle outbreak that affected most of the subalpine forests of central-western and northwestern Colorado in the 1940s (Hinds et al. 1965).

Outbreaks of spruce beetle, the most damaging insect

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FIG. 1. 1986 view of the Ripple Creek Pass area (near stand W3) of White River National Forest, Colorado, where nearly all the dominant Engelmann spruce were killed during the 1940s spruce beetle outbreak.

of the subalpine zone, are triggered by blowdowns or the accumulation of logging debris (Schmid and Frye 1977). Endemic spruce beetle populations infest fallen trees and scattered live trees, but during outbreaks can kill most canopy spruce over extensive areas (Schmid and Frye 1977). Beetles partially consume the phloem and transmit several fungi that cause occlusion of the outer xylem. It appears that spruce beetles preferentially attack slow-growing, large-diameter trees that are relatively free of lower branches. Spruce <10 cm in diameter are not usually attacked. In unusually severe outbreaks, the beetle attacks and kills lodgepole pine as well as spruce (Schmid and Frye 1977).

In 1939 a strong windstorm blew down extensive patches of subalpine forest in western Colorado, thus promoting the growth of endemic spruce beetle populations into the largest recorded epidemic of this century. By 1952, when the epidemic subsided, 10.1×10^6 m^3 (4.3×10^9 board feet) of timber had been killed (Massey and Wygant 1954). Three-quarters of this mortality was in White River National Forest, where an estimated 290,000 ha were devastated, and the remainder in Grand Mesa, Routt, and Arapaho National Forests (Hinds et al. 1965, Cahill 1977). Most beetle-killed spruce remain standing for many years so that the severity of the outbreak was still evident at the time of our sampling >40 yr later (Fig. 1).

In this paper we examine stand responses for six stands in the areas affected by the 1940s spruce beetle outbreak. In relation to canopy disturbance by a spruce beetle outbreak, we sought answers to the following questions: How are stand age and size structures altered? Does the outbreak retard the replacement of lodgepole pine by spruce and fir by permitting new seedling establishment? Or, does it accelerate successional replacement by the more shade-tolerant species? Is the response to the disturbance largely new seedling establishment or accelerated growth (i.e., releases) of already-established trees? Is the disturbance more favorable to recruitment of fir or spruce into the main canopy?

STUDY SITES

For sampling, we selected eight stands in subalpine forests located on both the western and eastern slopes of the northern Colorado Rocky Mountains (Fig. 2). Stands were chosen to represent the complete disturbance gradient—from severe, to moderate, to little-or-no disturbance—by the 1940s outbreak, and to include pure spruce and fir old-growth stands as well as late seral stands with lodgepole pine present. Six of the stands are in areas reported to have been affected by the 1940s outbreak in Forest Service reports (Hinds et al. 1965, Cahill 1977). Each stand sampled was homogeneous in terms of the degree of attack, as inferred from the number of dead-standing and fallen trees, but among sampled stands the apparent degree of attack ranged from severe to slight. For comparison with the beetle-attacked stands, we also sampled two stands in an area of no apparent or known history of spruce beetle outbreaks. Although these two stands were labelled controls and were essential for comparing tree growth patterns in stands not affected by an epidemic, the heterogeneity of forest structure within the subalpine forests was too great for them to serve as experimental controls. Consequently, published tree age and size data from numerous other stands (Whipple and Dix 1979, Peet 1981, Veblen 1986*a*, *b*, Aplet et al.

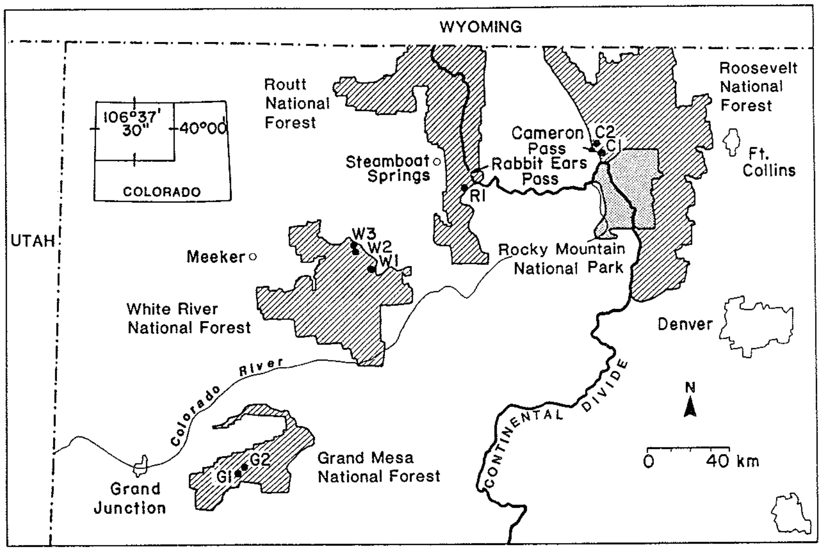

FIG. 2. Map of northwestern Colorado showing the locations of stands sampled. Abbreviations are: C1, Cameron Pass; C2, Blue Lake; R1, Walton Creek; W1, Trappers Lake; W2, Lily Pond; W3, Ripple Creek Pass; G1, Cottonwood Lake; G2, Big Creek Reservoir.

1988) were also used in comparing stand structures of affected and unaffected stands. Three stands are in White River, two in Grand Mesa, one in Routt, and two in Roosevelt National Forests. No spruce beetle outbreaks have been reported for the two areas sampled in Roosevelt National Forest, which are the two areas we used as controls. During the 1940s outbreak, at least 50% of the merchantable volume of spruce in Grand Mesa National Forest, and >90% in White River National Forest, were killed (Schmid and Hinds 1974; Fig. 1). Near our sampling site in Routt National Forest, 43% of the spruce >20 cm diameter at breast height (dbh) were killed (Hinds et al. 1965). Major outbreaks during the latter half of the 19th century are also reported for the White River and Grand Mesa National Forests (Schmid and Hinds 1974).

The two control stands in Roosevelt National Forest, Cameron Pass (C1) and Blue Lake (C2), are in the Front Range on soils derived from glacial till. The three White River sites, Trappers Lake (W1), Lily Pond (W2), and Ripple Creek Pass (W3), and the two Grand Mesa sites, Cottonwood Lake (G1) and Big Creek Reservoir (G2), are located on ≈3000 m high basaltic plateaus. The Routt stand, Walton Creek (R1), is in the Park Range where soils are derived from gneiss and schist (Chronic and Chronic 1972). Soils at all sites are shallow and coarse-textured, and are classified as Cryoboralfs, Cryocrepts, and Cryorthents (Johnson and Cline 1965).

The stands are on various aspects at elevations from ≈2970 to 3300 m (Table 1), but elevation, degree of mortality, and stand structure were relatively uniform within each stand over an area >4 ha. Precipitation in the subalpine zone falls primarily as snow and secondarily in summer convective storms. Mean annual precipitation in the Colorado subalpine zone varies from 600 to 1000 mm (National Oceanic and Atmospheric Administration 1971). The higher elevation sites have somewhat cooler and more mesic climates. All sites are characterized by short summers, typically with <60 frost-free days (Barry 1972). Understory composition and topographic position allow the ranking of the sites according to soil moisture availability as follows (from wettest to driest): C2, G2, W2, R1, G1, W3, W1, and C1.

All sites were dominated by Engelmann spruce and subalpine fir (Table 2). The two driest stands (C1 and W1) also included numerous lodgepole pine. Abundant charcoal occurred at control site C1, which had the typical age and size structure of a late seral (i.e., ≈200 yr old) post-fire stand on a xeric site. The pioneer lodgepole pine persisted on such sites, but it is gradually being replaced by spruce and fir (Whipple and Dix 1979, Veblen 1986*a*). Control site C2, where no charcoal could be found, had the typical size and age structure of an old-growth mesic spruce–fir stand. Spruce dominated in basal area, and both species were represented by trees of all ages (Whipple and Dix 1979, Veblen 1986*a*, Aplet et al. 1988).

METHODS

Field methods

Each of the eight stands was sampled in 1987 with 10 plots systematically located at 20-m intervals along a 300 m long transect running upslope. This plot placement assured that the samples were not too localized. Plot size varied from 10 × 10 to 10 × 30 m according to the density of live trees, so that each plot contained

TABLE 1. Site factors for the stands sampled.

Stand	Elevation (m)	Aspect	Slope (degrees)	Severity of the 1940 outbreak
Roosevelt National Forest (controls)				
Cameron Pass (C1)	3040	South	0–14	None
Blue Lake (C2)	3020	South	0–2	None
White River National Forest				
Trappers Lake (W1)	3000	North	11–27	High
Lily Pond (W2)	2970	Variable	0–14	High
Ripple Creek (W3)	3150	Northwest	0–5	High
Routt National Forest				
Walton Creek (R1)	3050	Northeast	2–10	Low
Grand Mesa National Forest				
Cottonwood Lake (G1)	3300	Northwest	0–17	None*
Big Creek (G2)	3080	Northeast	2–17	Moderate

* Although a spruce beetle epidemic was reported for this general area (Schmid and Hinds 1974), this stand was not significantly affected.

≈20 live trees. All saplings (<4 cm dbh but ≥1.4 m tall) were counted by species. All fallen trees >15 cm dbh that intercepted the transect tape bisecting each plot were identified by species and their dbh's were measured. Species and dbh were recorded for all trees ≥4 cm dbh, both live and dead standing. Because most Engelmann spruce killed by spruce beetle remain dead standing for many decades (Hinds et al. 1965), the density and basal area of dead-standing trees are good indicators of the amount of beetle-caused mortality. The spruce killed in the White River outbreak have been falling at the rate of 1.5% per year (Schmid and Hinds 1974). Eighty-five percent of the dead spruce from an earlier outbreak in Utah were still standing 25 yr after the outbreak (Mielke 1950).

Tree seedling (<1.4 m tall) densities were sampled with ten 1 × 1 m quadrats randomly located in each plot. Half of the quadrats were randomly located to each side of the transect tape in each plot. Seedlings were counted in height classes of <20 cm and 20–140 cm.

In each plot, increment core samples for tree aging were extracted at a height of ≈30 cm above the ground from all live trees >4 cm dbh. Approximately ten short seedlings (≈10 cm tall), tall seedlings (≈80 cm tall), and saplings of each species were cut at the base for aging. In addition to the cores taken from all trees in the 10 plots in each stand, supplemental cores were taken from the largest, and presumably oldest, live trees in each stand to develop long ring-width chronologies. Two cores were extracted at a height of 1.1 m from ≈10 of the largest trees of each species in each stand. These ring-width chronologies allowed examination of past changes in radial growth patterns.

Dendroecological analyses

All cores were mounted and sanded with successively finer grades of sand paper following the procedures of Stokes and Smiley (1968), and annual rings were counted under stereomicroscopes. Because of rotten centers, small numbers of sampled trees in each stand could not be aged (see Fig. 4 for percentages aged in each stand), but their dbh's are included in the dbh frequency distributions (Fig. 3). Due to the variable periods required for trees to reach coring height, tree ages are given as age at coring height. Years were recorded in which growth releases were initiated. A growth release was defined as a 250% increase in mean ring width when means of consecutive groups of five years were compared. Trees that experienced rapid initial growth, presumably reflecting establishment under relatively open conditions following disturbance, were also counted as "releases." Cores from such trees were identified by their consistently wide rings over the initial 10–20 yr of growth. Release data are summarized as the percentage of those trees surviving to 1987 that showed a release in a given year.

Mean ring-width chronologies were developed separately from ≈20 randomly selected trees of each species in each stand, and from ≈20 cores from the subjectively selected older trees. The randomly selected trees included many small subcanopy trees, which were more likely to respond to the 1940s outbreak, whereas the subjectively selected older trees, most of which were canopy trees, permitted examination of the long-term history of each stand. For the chronologies of the randomly selected trees, only cores >60 yr old were used, thus assuring a constant sample size for at least the 1927–1986 period. All the cores from the older trees were visually cross-dated using the techniques of Stokes and Smiley (1968). Ring widths were measured to the nearest 0.01 mm with a Henson computer-compatible incremental measuring machine. The computer program COFECHA (Holmes 1983) was used to detect measurement and cross-dating errors, and cores containing such errors were corrected or removed from the data set. COFECHA tests for errors by computing correlation coefficients between individual series and the master chronology for each species.

Ring-width chronologies were standardized with the programs INDEX and SUMAC to reduce ring-width variances among and within cores (Fritts 1976, Graybill 1979). Standardization involves fitting the observed ring-width series to a curve or a straight line and computing an index of the observed ring widths divided by the expected value. This reduces variances among cores, and transforms ring widths into dimensionless index values. Thus, standardization permits computation of average tree-ring chronologies without the average being dominated solely by the faster growing trees with large ring widths. Following extensive experimentation with the common alternatives used in standardization (horizontal or inclined straight lines, cubic spline functions, and exponential or polynomial curves), the horizontal straight line passing through the mean ring width was selected as the most useful standardization procedure (Veblen et al., *in press*). Thus, the ring-width index is the actual ring width in a core, for a particular year divided by the mean ring width of the entire core. The horizontal straight-line fit does not detrend the series. It facilitates the detection of deviations from the average growth rate, and is particularly useful in identifying long periods of release such as those expected to be associated with a major canopy disturbance.

TABLE 2. Tree composition of the stands sampled.

Stand / Species	Basal area (m^2/ha) Live	Basal area (m^2/ha) Dead standing	Density (no./ha) Live	Density (no./ha) Dead standing
Cameron Pass (C1)				
Pinus contorta	18.1	2.1	175	31
Abies lasiocarpa	13.1	5.4	888	187
Picea engelmannii	24.7	0.3	600	19
Blue Lake (C2)				
Abies lasiocarpa	11.2	8.2	943	129
Picea engelmannii	30.9	8.8	1079	85
Trappers Lake (W1)				
Pinus contorta	3.9	14.1	59	208
Abies lasiocarpa	13.5	2.0	1105	87
Picea engelmannii	2.5	8.2	418	132
Lily Pond (W2)				
Abies lasiocarpa	20.5	3.9	1155	85
Picea engelmannii	11.6	15.3	485	80
Ripple Creek Pass (W3)				
Abies lasiocarpa	30.3	5.7	1650	100
Picea engelmannii	6.4	8.9	515	80
Walton Creek (R1)				
Abies lasiocarpa	35.9	3.8	952	171
Picea engelmannii	10.3	9.2	348	71
Cottonwood Lake (G1)				
Abies lasiocarpa	22.3	8.5	1015	305
Picea engelmannii	35.0	0.5	695	60
Big Creek Reservoir (G2)				
Abies lasiocarpa	24.9	11.3	727	195
Picea engelmannii	21.8	2.1	441	32

RESULTS

Disturbance severity

Tree mortality patterns indicate that the greatest severity of the 1940s spruce beetle outbreak occurred in the three White River stands. All three stands contained more dead-standing basal area than live basal area of spruce (Table 2). Virtually all dead-standing spruce as well as fallen trees were engraved with beetle galleries. In subalpine forests not affected by recent spruce beetle outbreaks, fallen fir trees are usually more abundant than fallen spruce trees (Veblen 1986*b*). Thus the greater numbers of intercepted spruce logs in all three White River stands further indicates the high severity of the 1940s outbreak (Table 3). In all stands except the White River stands, fallen fir trees were more abundant than fallen spruce trees. Although a few fallen trees at each site could not be identified (Table 3), they were not sufficiently abundant to alter the described patterns.

At control site C1, dead-standing trees and logs of spruce were rare, which is consistent with the lack of any recent spruce beetle outbreaks (Tables 2 and 3). At control site C2, the high basal area of dead-standing spruce results from a few large dbh dead trees (Table 2; Fig. 3). These large dead trees were engraved with beetle galleries and may have been killed by the endemic spruce beetle population, but there was no evidence of an epidemic.

At Walton Creek (R1) the live and dead-standing basal areas of spruce were about the same, suggesting an outbreak of low-to-moderate intensity (Table 2). Fallen spruce trees in stand R1 were scarce but large (Table 3). In stand G1 on Grand Mesa, where the 1940s outbreak was reported to be less severe than in White River National Forest (Schmid and Hinds 1974), basal area of dead-standing spruce was low and intercepted fallen spruce trees were scarce. These data imply that stand G1 was not significantly affected by the 1940s outbreak. For stand G2, also on Grand Mesa, dead-standing basal area of spruce was low, but the abundance of large fallen spruce trees is consistent with a recent, but moderate, outbreak (Tables 2 and 3).

Effects on stand structure

Seedlings and saplings.—Spruce and fir seedlings can be very slow growing, and consequently not all seedlings would have established since the spruce beetle outbreaks of the 1940s. However, the age ranges of

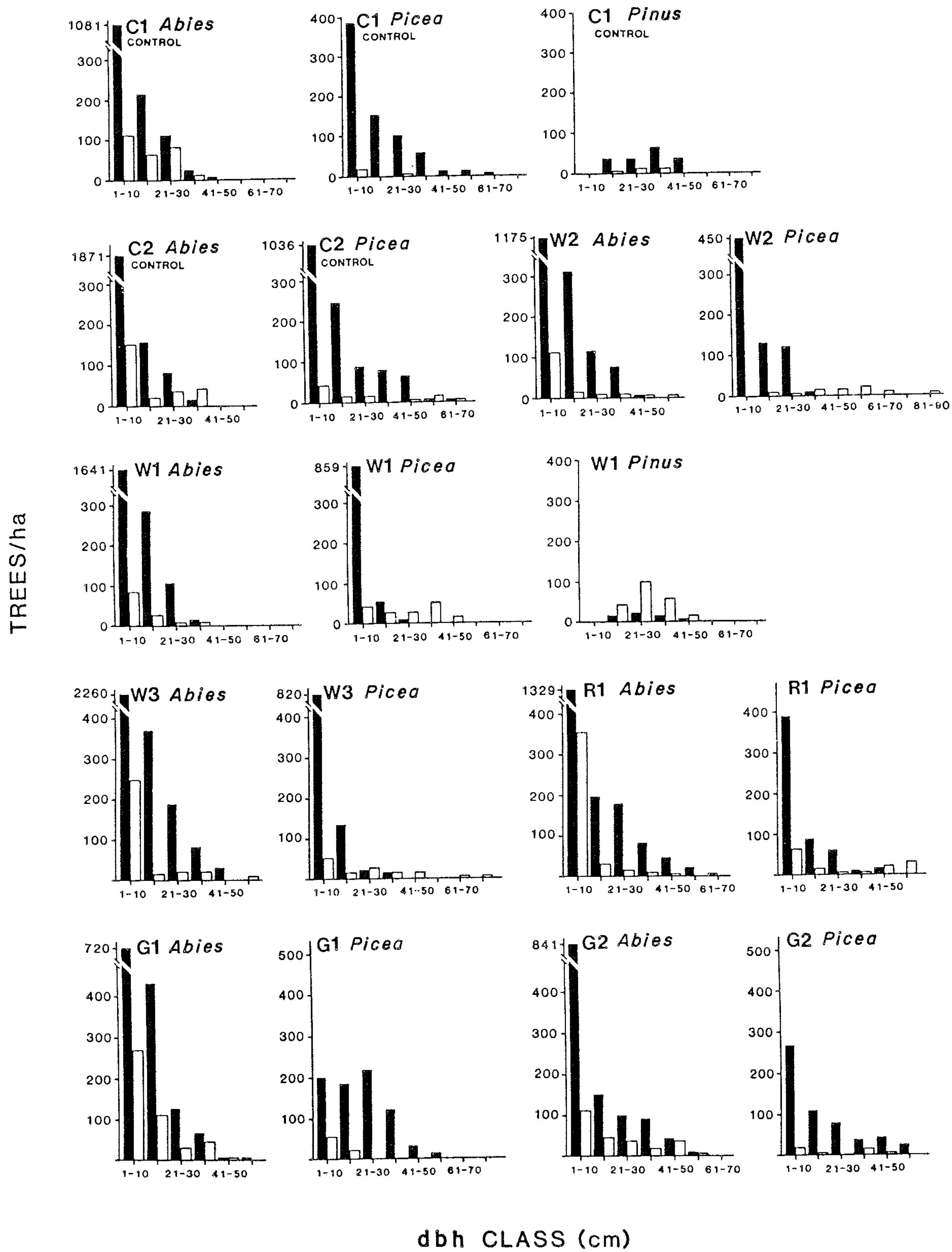

FIG. 3. Frequency distributions of live (solid bars) and dead (open bars) trees in 10 cm diameter-at-breast-height (dbh) classes for each tree species occurring in each of the eight stands. The dbh frequency distributions for live trees include both aged and unaged trees. Stand abbreviations as in Fig. 2.

TABLE 3. Numbers and median diameter at breast height (dbh) of fallen trees ≥15 cm dbh intercepted by transects in each stand sampled.

	Pinus contorta		*Picea engelmannii*		*Abies lasiocarpa*		Unidentified	
	No.	dbh	No.	dbh	No.	dbh	No.	dbh
Stand								
Cameron Pass (C1)	2	18	0	0	3	16	0	0
Blue Lake (C2)	0	0	8	39	14	23	0	0
Trappers Lake (W1)	25	25	19	26	6	19	7	31
Lily Pond (W2)	0	0	24	33	5	23	2	23
Ripple Creek Pass (W3)	0	0	20	26	10	21	6	20
Walton Creek (R1)	0	0	3	45	5	37	2	26
Cottonwood Lake (G1)	0	0	1	26	8	24	3	28
Big Creek Reservoir (G2)	0	0	8	40	27	37	3	34

seedlings indicated that nearly all short seedlings (<20 cm tall) in all stands had established since the 1940s outbreak (Table 4). In contrast, many tall seedlings (20–140 cm high) and saplings pre-dated the 1940s outbreak.

Although canopy disturbance by beetles might be predicted to favor tree seedling establishment, the data on abundances and ages of seedlings and saplings do not clearly demonstrate an increase in establishment rate. Seedlings were not consistently more abundant in the affected stands (Table 4). Fir seedlings, for example, were most abundant in severely disturbed stand W1, but in the other severely disturbed stands (W2 and W3) they were less abundant than in control stand C2 and the moderately disturbed stand R1. There was, however, a tendency for the ages of saplings to be younger in most of the more severely disturbed stands (e.g., stands W1, W2, and G2). This could indicate either new establishment of seedlings following the beetle outbreak or growth of the older saplings into the tree size class following the beetle outbreak. In general, however, if canopy disturbance favored seedling establishment of fir and spruce, it was not obvious ≈40 yr later. The absence of seedlings and saplings of lodgepole pine in stand W1 indicates that, despite the severe canopy disturbance, there was little or no new establishment of this shade-intolerant species.

Tree age and size structure.—In control stand C1 lodgepole pine occurred as a non-regenerating population ranging from 111 to 191 yr old (Fig. 4). In this first-generation post-fire stand, fir and spruce trees were relatively scarce in age classes younger than 100 yr. Dead-standing fir and spruce were mostly small trees, indicating that the mortality was the result of thinning of suppressed trees rather than canopy tree mortality (Fig. 3).

In control stand C2 fir and spruce had all-aged tree age distributions (Fig. 4 and Table 4). Although both species attained ages >300 yr, spruce dominated the age classes >200 yr and the dbh classes >30 cm (Figs. 3 and 4), as is typical for old-growth spruce–fir forests (Veblen 1986*b*). In contrast to stand C1, some of the dead spruce were large trees, which may have died from senescence and (/or) endemic beetle attack.

In stand W1 lodgepole pine occurred as a small population ranging in age from 216 to 261 yr (Fig. 4). This tree age distribution and the lack of saplings and short seedlings indicate that lodgepole pine seedlings have not become established since the 1940s outbreak. The large sizes of the beetle-killed lodgepole pine imply that prior to the outbreak it was similarly not regenerating (Fig. 3). In contrast, subalpine fir was abundant in tree age classes <160 yr (Fig. 4). Both fir and spruce had all-aged tree distributions prior to the outbreak. Maximum tree ages for fir and spruce in stand W1 were 251 and 220 yr, respectively. These age data, the abundance of charcoal at the soil surface, and the presence of the remnant lodgepole pine population indicate that stand W1 was a first-generation post-fire stand prior to the beetle outbreak. In subalpine forests, initial post-fire colonization by spruce tends to be more abundant than fir, which results in more abundant spruce than fir in the older age classes and larger size classes (Whipple and Dix 1979, Peet 1981, Veblen 1986*a*). However, in stand W1 beetles had killed most of the spruce >100 yr old and >20 cm dbh (Table 3 and Fig. 3), so that the typical relationship of fir–spruce abundances was reversed.

In stands W2 and W3 at White River and stand R1 in Routt National Forest, spruce and fir also had all-aged tree populations including young seedlings (Fig. 4 and Table 4). Again, the greater abundance of fir in age classes >140 yr and size classes >30 cm dbh, compared to spruce, appears to be a result of beetle-caused mortality of the older spruce (Fig. 3 and 4). This is also reflected by the abundance of dead-standing spruce >20 cm dbh (Fig. 3).

In stand G1 on Grand Mesa, which was not severely disturbed by the 1940s outbreak, tree age distributions for both spruce and fir were broadly bell-shaped (Fig. 4), and seedlings and saplings were relatively scarce (Table 4). The proportions of large and old fir and spruce are typical of stands not significantly disturbed by spruce beetles. Here, spruce was the more abundant

TABLE 4. Tree seedling and sapling densities and median ages. Age was determined at ground level for 8 to 15 samples. Age ranges are given in parentheses below each median.

	Short seedlings <20 cm tall		Tall seedlings 20–140 cm tall		Saplings >140 cm tall but <4 cm dbh	
	Age (yr)	Density (no./ha)	Age (yr)	Density (no./ha)	Age (yr)	Density (no./ha)
Cameron Pass (C1)						
Abies lasiocarpa	19 (5–23)	800	113 (59–135)	2700	120 (97–141)	1175
Picea engelmannii	13 (8–21)	100	109 (76–134)	300	140 (119–146)	144
Blue Lake Trail (C2)						
Abies lasiocarpa	12 (7–21)	2500	79 (49–123)	5400	125 (83–143)	1179
Picea engelmannii	12 (8–23)	2500	59 (35–108)	1800	96 (62–191)	443
Trappers Lake (W1)						
Abies lasiocarpa	11 (7–19)	14600	28 (19–35)	6700	50 (29–128)	936
Picea engelmannii	16 (8–28)	600	37 (15–45)	2800	37 (27–125)	505
Lily Pond (W2)						
Abies lasiocarpa	N.D.*	1800	52 (22–81)	700	35 (28–72)	525
Picea engelmannii	8 (5–21)	1300	20 (11–43)	600	33 (22–67)	225
Ripple Creek Pass (W3)						
Abies lasiocarpa	21 (10–38)	1300	82 (46–95)	5100	76 (46–103)	1270
Picea engelmannii	25 (14–41)	600	52 (31–123)	3100	92 (69–122)	470
Walton Creek (R1)						
Abies lasiocarpa	22 (11–26)	7100	68 (27–89)	5000	88 (61–120)	895
Picea engelmannii	24 (14–31)	3400	50 (27–66)	1100	78 (60–86)	205
Cottonwood Lake (G1)						
Abies lasiocarpa	19 (12–25)	900	90 (63–107)	2100	107 (68–134)	330
Picea engelmannii	22 (9–31)	200	61 (50–85)	0	104 (42–147)	65
Big Creek Reservoir (G2)						
Abies lasiocarpa	11 (5–23)	1400	51 (29–101)	1600	90 (31–118)	505
Picea engelmannii	16 (7–28)	200	41 (36–53)	500	90 (36–119)	109

* No data.

tree in the older age classes and larger dbh classes (Figs. 3 and 4). In contrast, in the beetle-disturbed stand G2, fir was the more common species in dbh classes >20 cm and age classes >160 yr old (Figs. 3 and 4).

Tree growth responses

In the three White River stands and in stand G2 on Grand Mesa there were dramatic increases in the percentages of trees released in the 1940s and 1950s in association with the beetle outbreak (Fig. 5). Subalpine fir, because of its abundance, is the best indicator of canopy disturbance. In stands W3 and G2 the increase in frequencies of released trees in 1939 and 1940 may be in response to the 1939 windstorm (see *Introduction*, above), while the increases beginning in the mid- to-late 1940s in all four stands correspond to the beetle outbreak. In comparison, neither of the control stands C1 or C2 shows a major increase in frequencies of released trees (Fig. 5), which implies neither stand has suffered a severe canopy disturbance during this ≈100-yr record of releases. There were much higher frequencies of trees released in stand C2 than in stand C1, as expected for an older stand in which the rate of treefall of large gap-producing individuals was higher (Fig. 5).

In stand G1 on Grand Mesa releases were not nec-

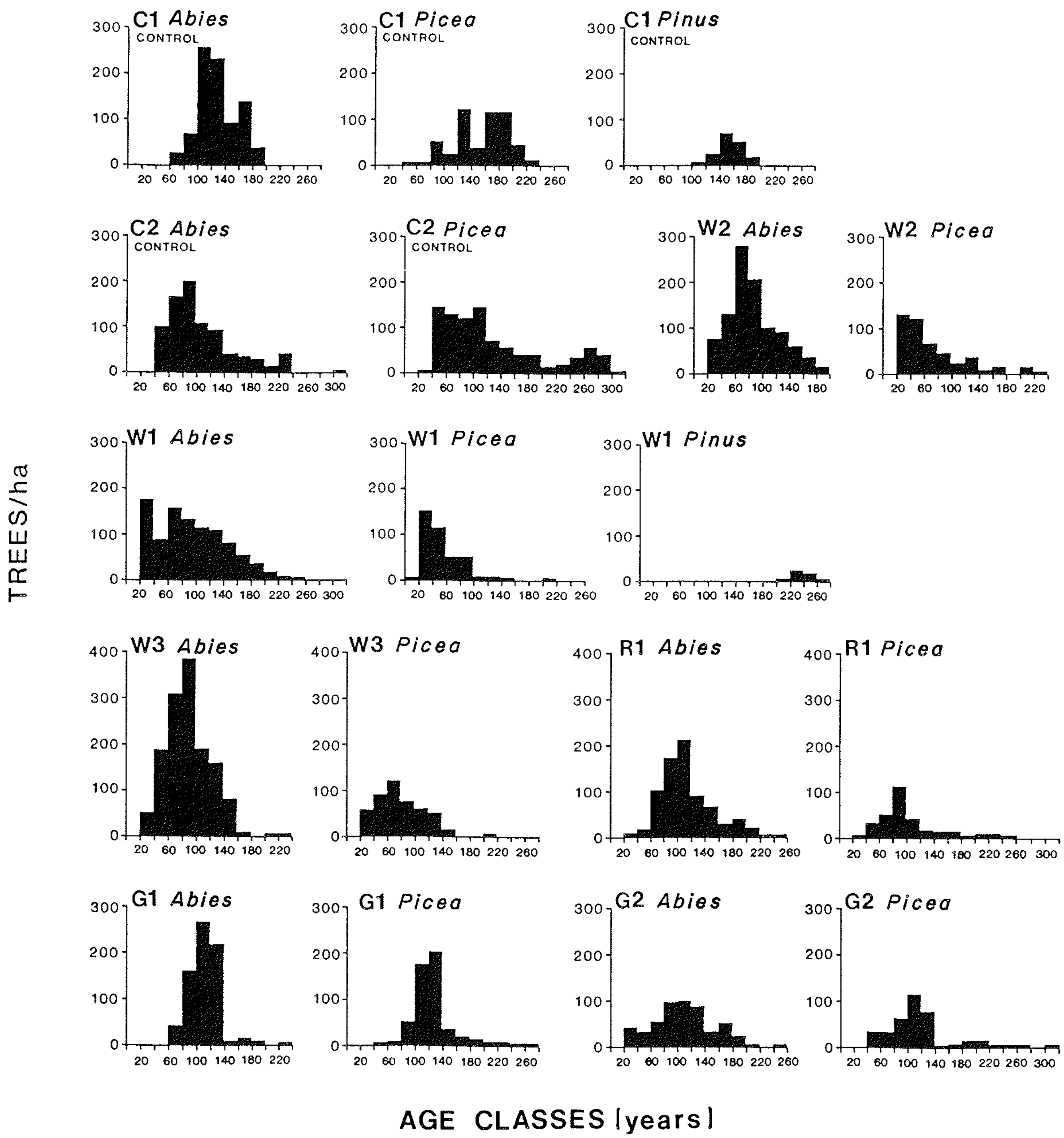

FIG. 4. Frequency distributions of trees ≥4 cm dbh in 20-yr age classes for each tree species occurring in each of the eight stands. Stand abbreviations as in Fig. 2. The percentage or trees in each sample that were successfully aged are: for Engelmann spruce 95% in W1, 97% in W2, 90% in W3, 89% in R1, 77% in G1, 86% in G2, 88% in C1, and 87% in C2; for subalpine fir 89% in W1, 84% in W2, 84% in W3, 80% in R1, 77% in G1, 86% in G2, 88% in C1, and 87% in C2; for lodgepole pine 85% in W1 and 96% in C1.

essarily more abundant during the 1940s than at other times during the past 100 yr, such as the 1880s or 1960s (Fig. 5). This is consistent with the lack of other evidence of disturbance by beetle outbreak despite the stand's location in a general area of moderate outbreak (Schmid and Hinds 1974). Stand R1, despite its location in an area of reported outbreak in the 1940s, showed only slight increases in frequencies of released trees beginning in the late 1940s. Here, the intensity of the 1940s outbreak was low, as judged from the scarcity of dead spruce, and would not have been detected from patterns of tree release alone.

In the chronologies derived from the randomly selected cores in the severely disturbed stands (W1, W2, and W3 in White River and in the moderately disturbed stand G2 on Grand Mesa), there were abrupt

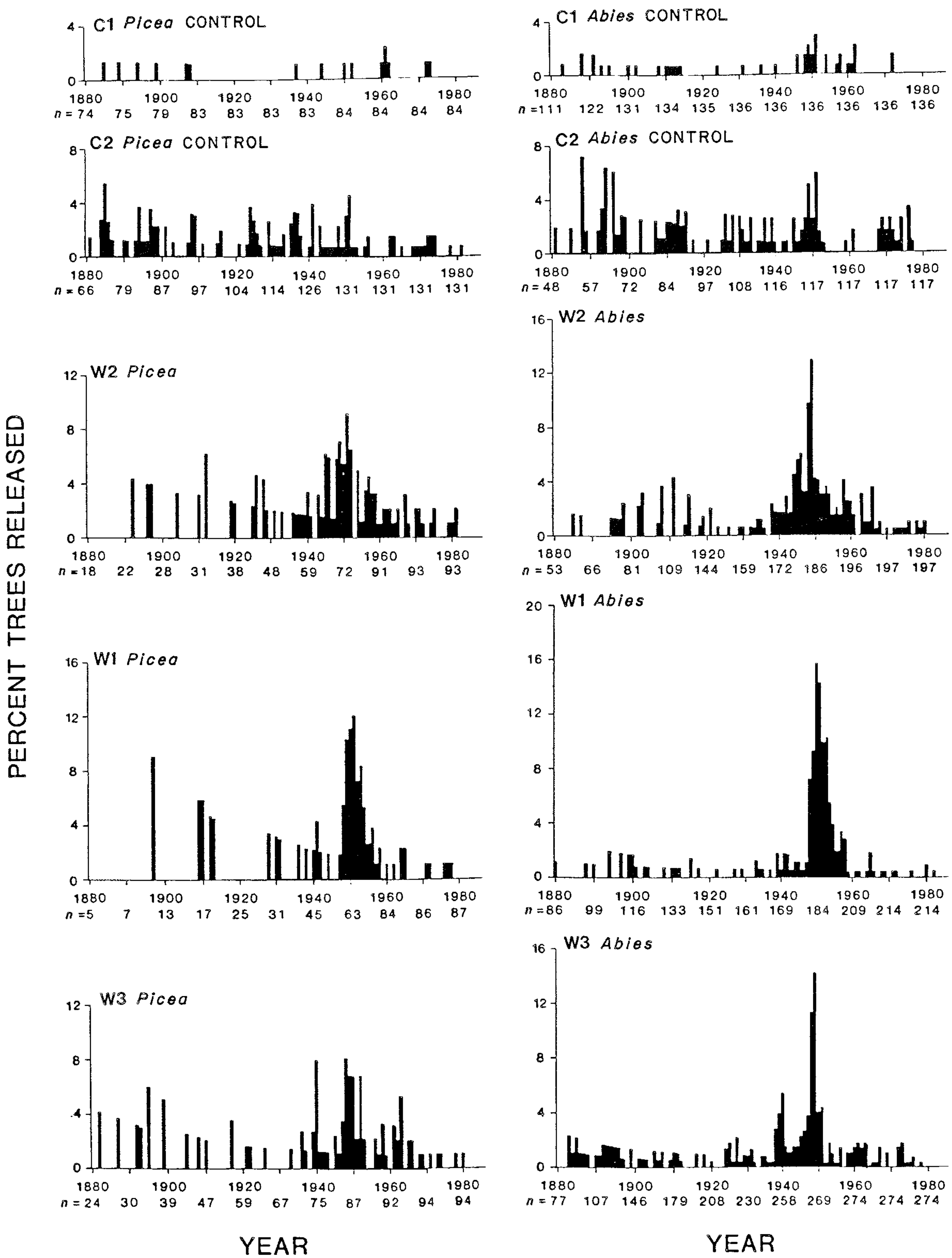

FIG. 5. Percentage of live trees released. A release is an increase in mean ring width of >250% when adjacent groups of five rings are compared. The number of surviving trees alive at the beginning of each decade is given by n. Stand abbreviations as in Fig. 2.

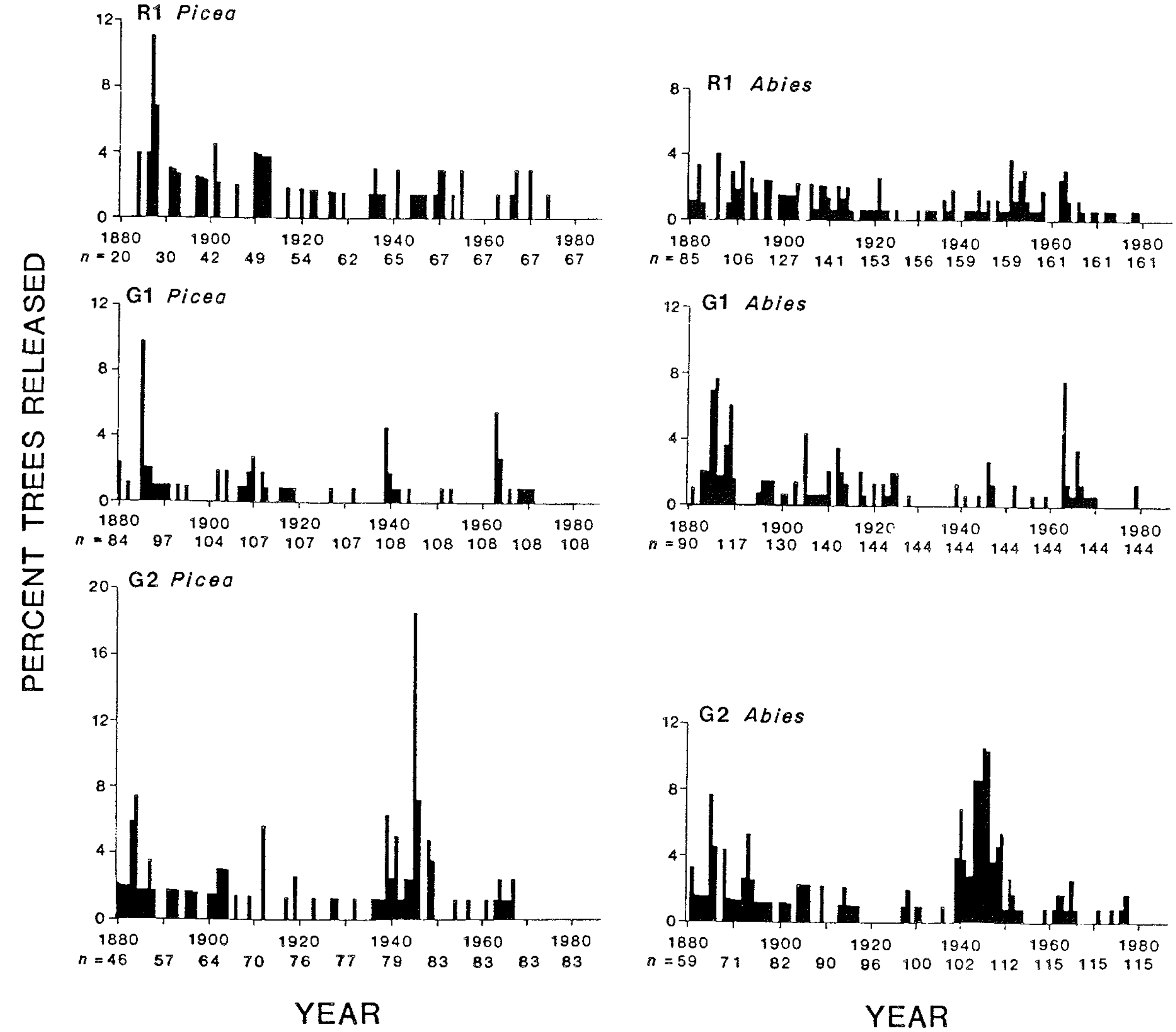

FIG. 5. Continued.

and sustained two- to five-fold increases in mean ring widths corresponding to the 1940s beetle outbreak (Fig. 6). Lodgepole pine in stand W1 showed the weakest response, as expected for trees that were predominantly canopy individuals at the time of the outbreak (Fig. 3). The more dramatic responses of fir and spruce reflect the position of many of these individuals in the subcanopy, where they would benefit more from the release of resources associated with the death of canopy trees. The increased growth rates which began in the 1940s persisted to 1986, the last year measured. In contrast, control stands C1 and C2 did not show major sustained increases in mean growth rates in the 1940s or 1950s (Fig. 6). Over the period from 1880 to 1986 fir in both control stands and spruce in control stand C2 showed increasing growth rates, reflecting the growth of previously suppressed subcanopy trees into the main canopy as old canopy trees died. Short periods (e.g., 5–10 yr) of accelerating growth rates of fir in stand C1 in the 1960s, and of both species in stand C2 in the 1950s and 1960s, may reflect small-scale wind disturbance. However, the magnitudes and durations of these accelerations are much less than those associated with beetle outbreak in stands W1, W2, W3, and G2.

The randomly selected trees in stand R1 showed increasing growth rates since the early 1940s, but not the dramatic increases seen in stands W1, W2, W3, and G2 (Fig. 6). This is consistent with an outbreak of low severity as judged from the number of dead-standing spruce (Table 2). However, the growth patterns of the randomly selected trees are not sufficient for certain identification of the 1940s outbreak in stand R1, as indicated by comparison with control stand C2 (Fig. 6). On Grand Mesa stand G1 lacked any increase corresponding to the 1940s outbreak, which is consistent with the scarcity of dead spruce in that stand (Tables 2 and 3).

The long chronologies developed from the subjec-

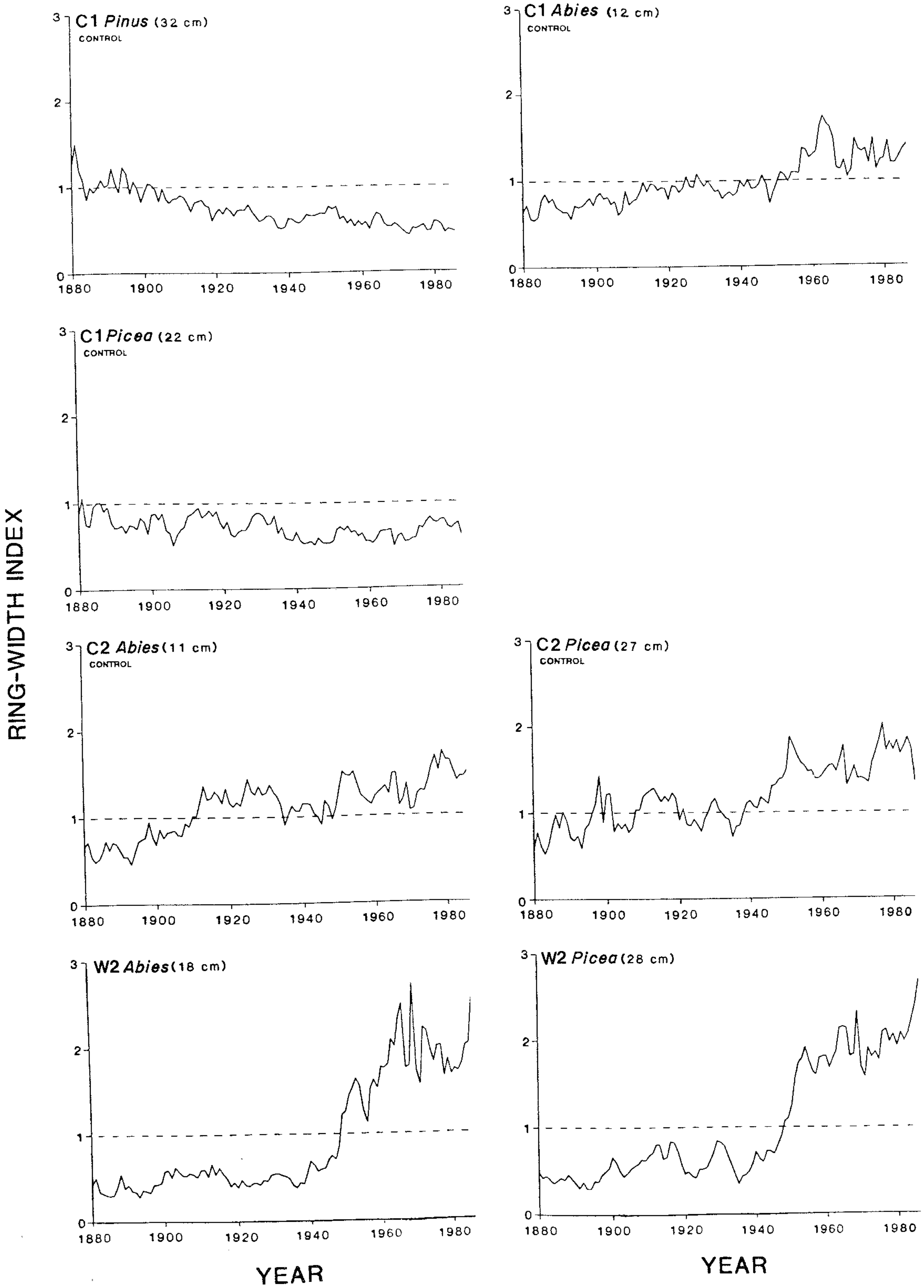

FIG. 6. Mean ring-width indices (actual ring width divided by mean ring width in that core) for randomly selected trees in each stand. The number in parentheses is the median diameter at breast height of the trees sampled. The number of cores used in the chronologies ranged from 10 to 20 for the period 1880–1926 and was 20 for the period 1927–1986 except for lodgepole pine in stand W1 where n = 10 for the entire chronology. Stand abbreviations as in Fig. 2.

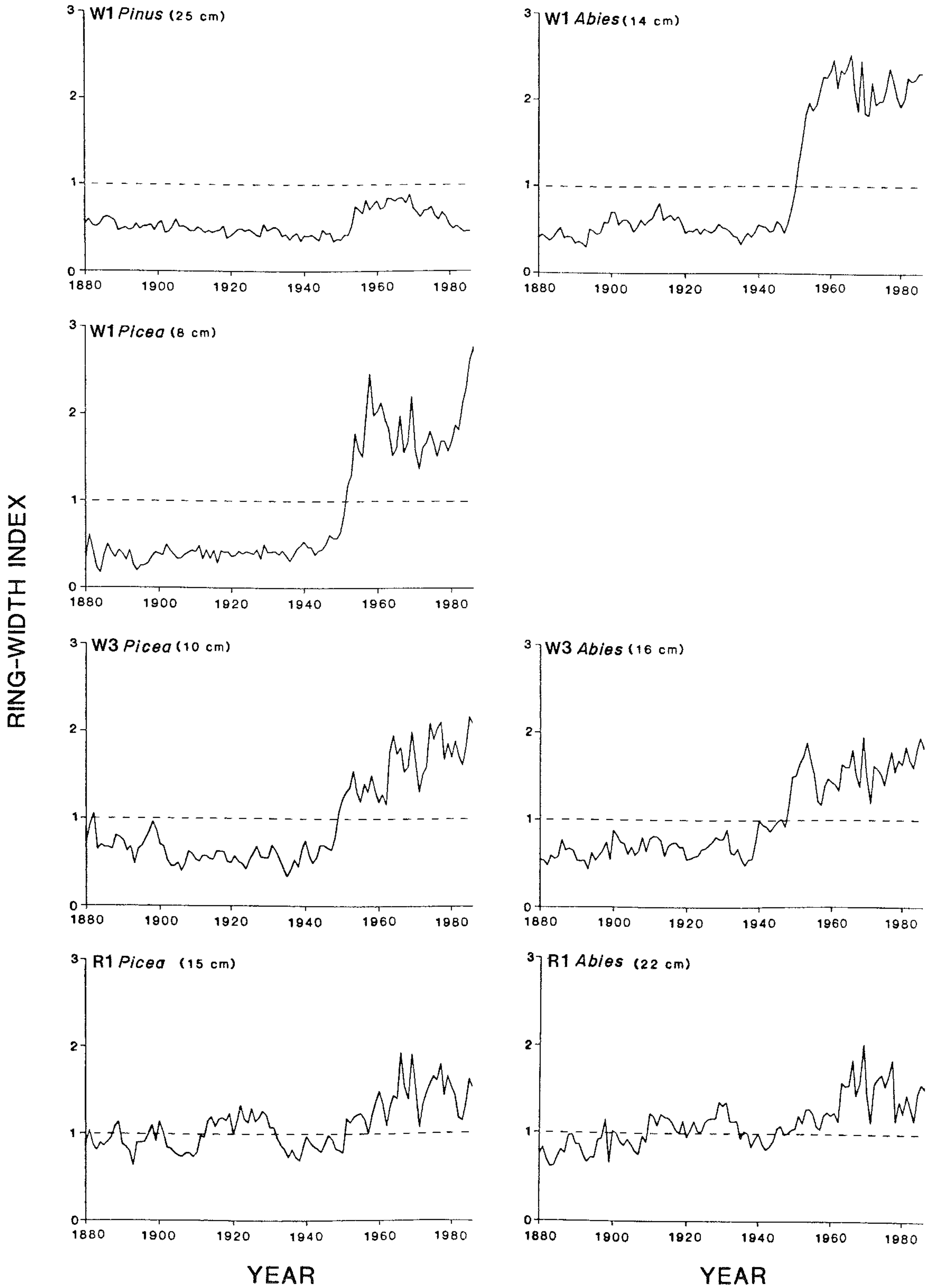

FIG. 6. Continued.

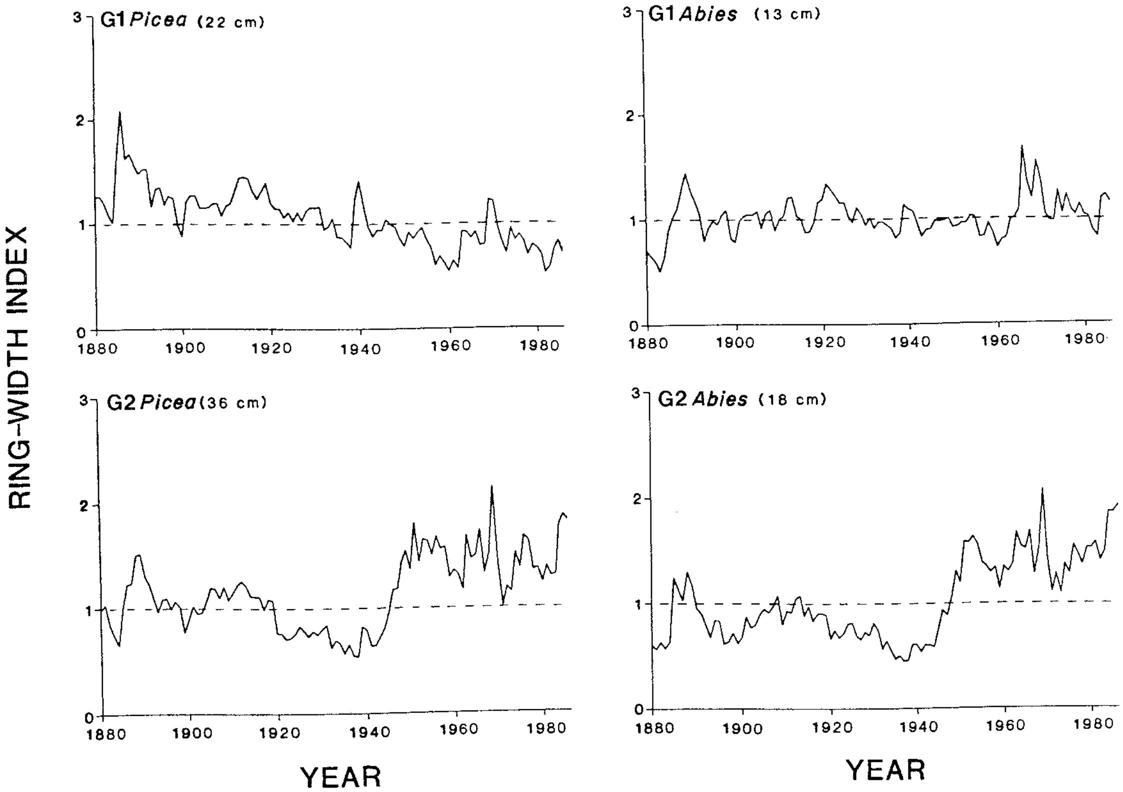

FIG. 6. Continued.

tively selected older trees allow examination of the responses of mostly canopy trees to the 1940s outbreak. In most stands the median dbh of trees used in the long tree-ring chronologies was two or more times as great as that of the median dbh of the randomly selected trees of the same species, which were mostly subcanopy trees (Figs. 6 and 7). The long chronologies further elucidate the patterns of stand development derived from age structures.

In control stand C1 the long chronologies for all three species indicate rapid initial growth rates, which declined dramatically as the stand developed (Fig. 7). This is the expected pattern for tree populations that began to establish soon after a stand-initiating fire. None of the species showed any abrupt and sustained acceleration in growth rate that could be associated with a major canopy disturbance.

In contrast, in control stand C2 neither spruce nor fir had the exponentially declining pattern of mean ring width expected for a post-fire population (Fig. 7). Fir had a slowly increasing average growth rate with increasing stand age. Spruce had a fluctuating growth rate that does not change markedly over the >300-yr record. In the late 17th and early 18th centuries there was a sustained period of above-average mean ring widths, which may indicate an early canopy disturbance such as a spruce beetle outbreak.

In stand W1 lodgepole pine initially grew rapidly, as expected for a post-fire population (Fig. 7). Its growth rate declined rapidly over the first 100 yr of stand development to a low but fluctuating rate. Given the large size of these trees at the time of the 1940s beetle outbreak, it is not surprising that the disturbance increased the mean growth rate only slightly. Spruce and fir in stand W1 had low growth rates until released by the 1940s outbreak. The length and magnitude of their growth accelerations were less than those for the randomly selected trees (Figs. 6 and 7). This is consistent with the mainly subcanopy positions of the randomly selected trees and the canopy stature of the older trees.

The low initial growth rates of the oldest trees in stands R1, G1, and G2 indicate that these are not post-fire stands (Fig. 7). In stands W2 and W3 it is likely that the oldest spruce were killed by beetles, which makes it difficult to determine if these stands were initiated by fire. Nevertheless, growth patterns imply that stand W3 is not a first-generation post-fire stand, while stand W2 may be. In stands W2 and W3 growth accelerations of the older trees clearly indicate the 1940s outbreak, but were generally less than those of the randomly selected trees. In stand G2 moderate growth-rate increases reflect the 1940s outbreak. In the slightly or unaffected stands G1 and R1, canopy tree growth rates do not reflect the 1940s outbreak. In stands R1, G1, and G2 there were major sustained growth-rate increases in the mid-19th century corresponding to a spruce beetle outbreak (Fig. 7). Extensive dead-standing spruce killed in this epidemic were reported for Grand Mesa and White River National Forest around the turn of the century (Sudworth 1900, Hopkins 1909).

Discussion

The 1940s spruce beetle outbreak of central-western and northwestern Colorado resulted in major changes in the structures of the most severely disturbed stands studied (i.e., stands W1, W2, W3, and G2). In particular, dominance in basal area shifted massively from spruce to fir, and average and maximum tree diameters, heights, and ages of stands were sharply reduced due to the mortality of the larger and longer lived spruce. In contrast, in the less disturbed stand R1 the effects of the outbreak were barely detectable. However, dates of death of the dead spruce, determined by cross-dating dead trees (Veblen et al., *in press*), are consistent with reports of the 1940s outbreak in this general area (Hinds et al. 1965). In contrast, although stand G1 was located in the general area affected by the 1940s outbreak (Schmid and Hinds 1974), it was not directly affected by the outbreak.

In White River National Forest, where the 1940s outbreak was most severe, the beetles killed many lodgepole pine in addition to the usual host species, Engelmann spruce (Schmid and Hinds 1974). The outbreak, however, did not result in significant new seedling establishment of the seral lodgepole pine in the sampled stands. The mortality of the pine plus the release of small spruce and fir resulted in a major shift in dominance towards the shade-tolerant tree species. A similar pattern of disturbance-mediated acceleration of succession also occurs following blowdown of lodgepole pine-dominated seral stands (Peet 1981, Veblen et al. 1989). The relative lack of bare mineral soil, possible lack of seeds, and the presence of advance regeneration of the shade-tolerant species are major reasons for the scarcity of new seedling establishment of lodgepole pine following a spruce beetle outbreak.

If the 1940s outbreak favored new establishment of spruce and fir seedlings, it was not detectable ≈40 yr later. Because spruce and fir seedling abundances are greatly influenced by variability in site factors (Knapp and Smith 1982, Alexander and Shepperd 1984), documentation of changes in establishment rates is not feasible without data on pre-disturbance seedling abundances.

The most striking response to the outbreak was the release of previously suppressed individuals of both fir and spruce. Following the 1940s outbreak, growth rates for both species have remained high in the severely affected stands for >40 yr. The responses to the mid-19th century outbreak indicate that growth rates may remain high for more than a century. Relative increases in growth rates were similar for both species and were clearly greater for small, subcanopy trees than for large-diameter canopy dominants. Thus the larger size of the non-host species following a beetle attack is not an overwhelming advantage, given the more rapid growth rates of subcanopy trees. As long as both species are abundant as trees <10 cm dbh in the subcanopy, spruce beetle outbreaks will favor the recruitment of both species into larger size classes. Because fir typically is more abundant than spruce as subcanopy trees (Peet 1981, Veblen 1986*b*), more of the former species can be expected to grow into larger size classes following an outbreak. However, given the greater longevity of spruce (Veblen 1986*b*), stands will continue to be codominated despite the recruitment of smaller numbers of spruce.

The importance of accelerated growth as opposed to new seedling establishment following a spruce beetle outbreak is a major contrast to what is usually observed following fires (Whipple and Dix 1979, Peet 1981, 1988, Veblen 1986*a*, Aplet et al. 1988). In particular, fires in the subalpine zone of the Colorado Rocky Mountains are largely stand-devastating disturbances that allow few if any trees to survive. Thus stand development following fire is dominated by new seedling establishment. Spruce and (/or) lodgepole pine typically dominate the initial several decades of post-fire seedling establishment. Fir is the least abundant species for several decades following fire, but because of its superior ability to establish on forest litter and under low light levels (Knapp and Smith 1982), it gradually increases in abundance during the course of stand development.

Whereas stand-devastating fires tend to favor dominance by spruce and (/or) lodgepole pine, severe beetle outbreaks shift dominance of these forests towards subalpine fir. Fir, however, becomes susceptible to pathogenic fungi as it reaches main canopy size (Schmid and Hinds 1974, Alexander 1987). Since many of the canopy fir die, subcanopy trees of both fir and spruce grow into the main canopy. Due to its greater maximum size and longevity, spruce eventually attains basal area dominance, and the stand becomes increasingly susceptible to a major spruce beetle outbreak (Schmid and Hinds 1974, Veblen 1986*b*, Alexander 1987). Given the high windspeeds of the southern Rockies and the susceptibility of spruce and fir to windthrow (Glidden 1981, Alexander 1987), an epidemic-triggering blowdown of the spruce-dominated stand is likely. Thus, in old-growth spruce–fir forests periodically affected by spruce beetle outbreaks, wave-like oscillations in basal areas are expected (Schmid and Hinds 1974).

Disturbance by spruce beetle outbreaks is widespread in the subalpine forests of the southern Rockies (Schmid and Frye 1977), and perhaps is as significant as fire in forest development (Baker and Veblen 1990). For example, the mid-19th century spruce beetle outbreak apparently was greater in extent than that of the

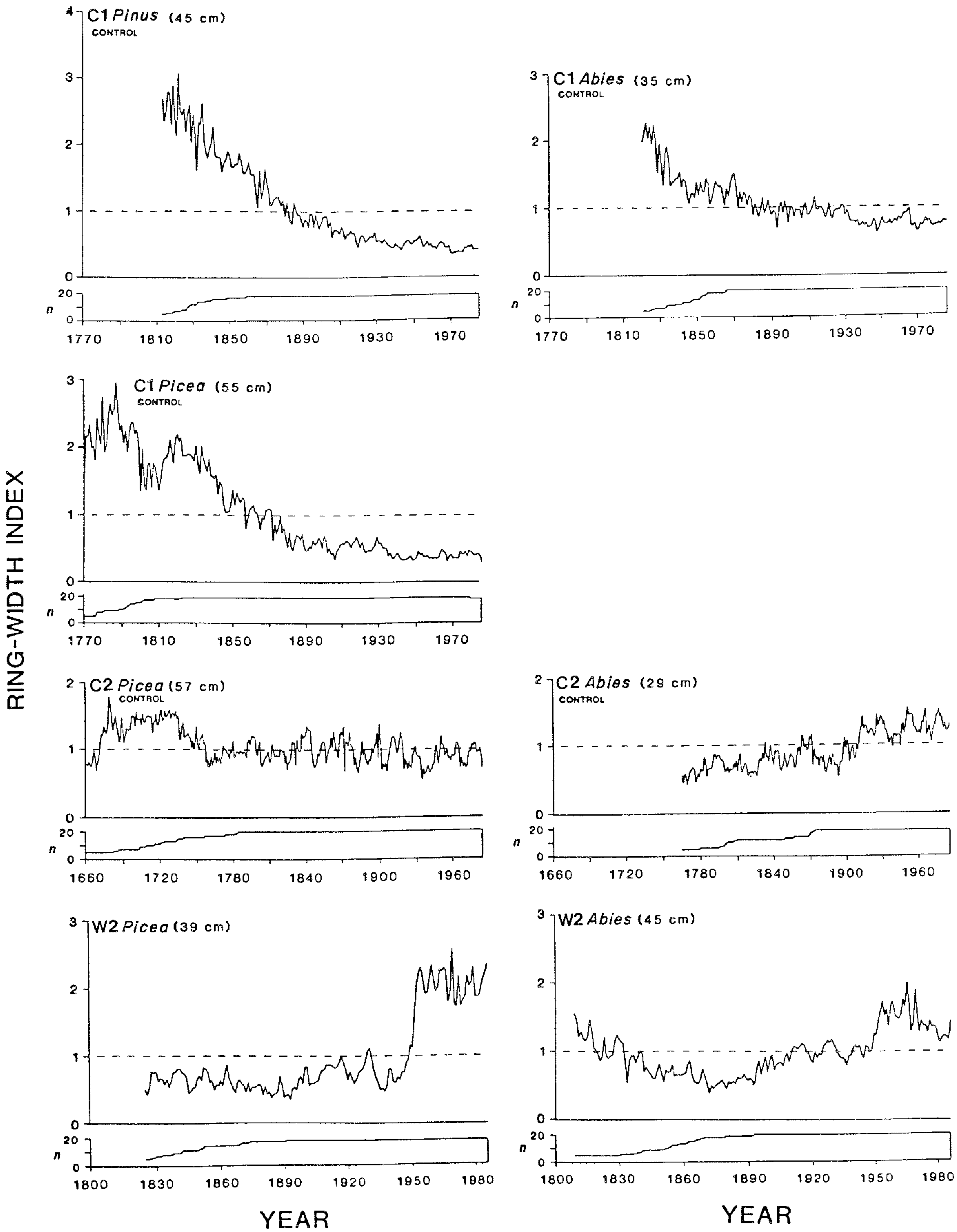

FIG. 7. Mean ring-width indices (actual ring width divided by mean ring width in that core) for selected older trees in each stand. Indices are plotted only for periods when $n \geq 5$. The median diameters at breast height of the trees sampled are given in parentheses. The varying number of cores contained in each chronology is indicated by the graph of n. Stand abbreviations as in Fig. 2.

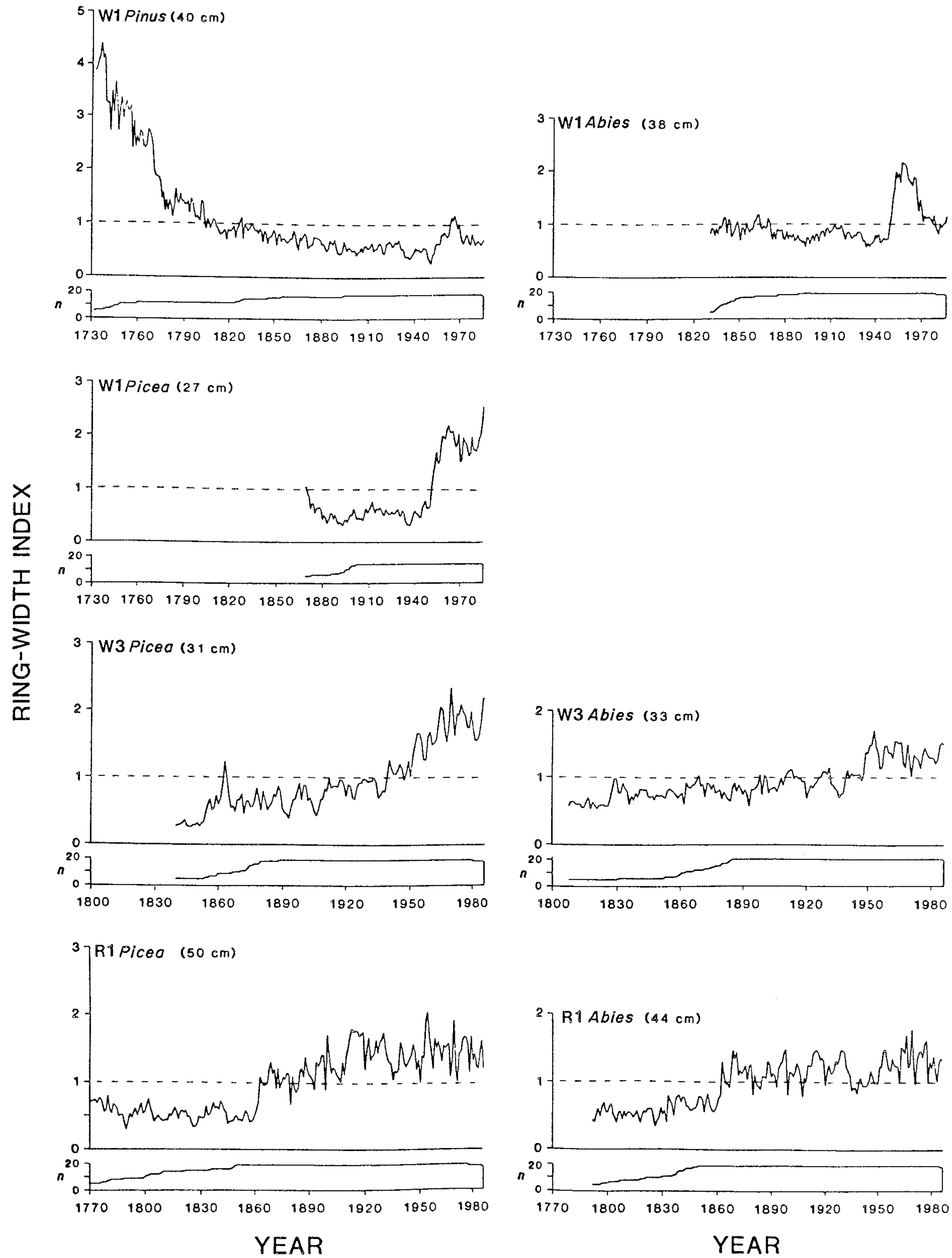

FIG. 7. Continued.

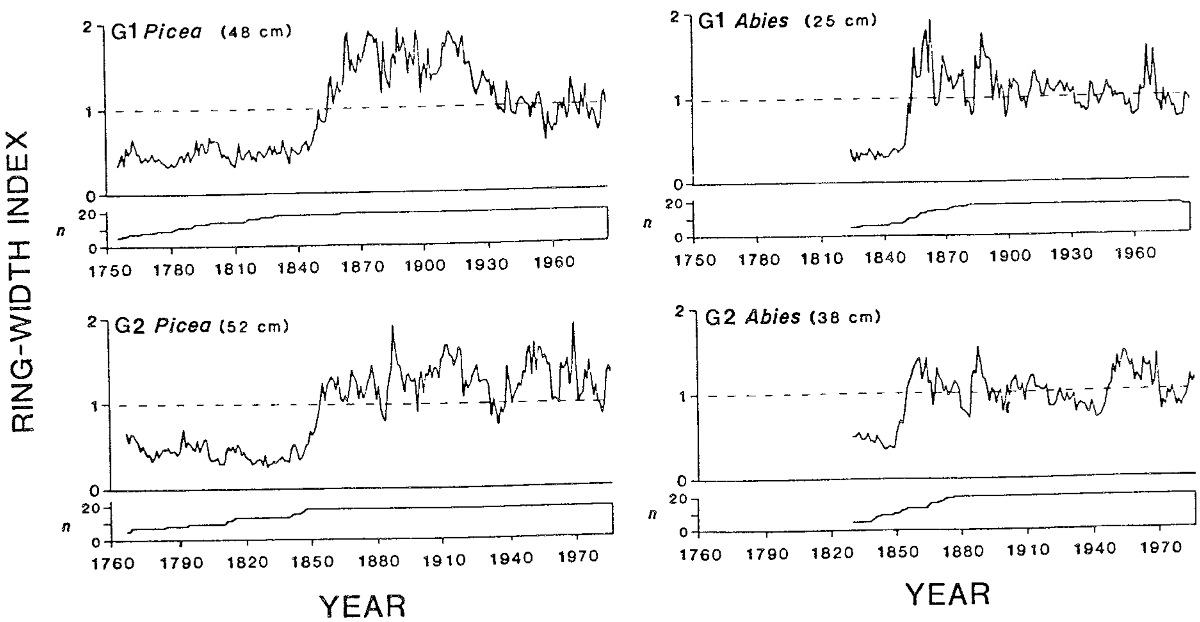

FIG. 7. Continued.

1940s, and affected forests from central New Mexico to northwestern Colorado (Baker and Veblen 1990, Veblen et al., *in press*). For many stands there is a high probability of severe disturbance by windstorm and spruce beetle during the slow development of an old-growth spruce–fir stand following wildfire. The effects of these canopy disturbances should be explicitly considered in explanations of the current structures of old-growth spruce–fir forests in the southern Rockies.

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